EVALUATION OF AN AURAL RECORD OF NOCTURNAL MIGRATION

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 \mathbf{I}^{N} an earlier paper (1959), we described a technique for detecting and automatically recording the calls of nocturnal migrants.

During the fall (August-October) of 1957, the spring (April-May) and fall of 1958, and the spring of 1959, we used this technique on 175 nights to collect data on bird migration in Champaign County, Illinois.

In the present paper we have placed emphasis on presentation of these audio data rather than on their interpretation. We have, however, attempted to determine how well the data compared with other types of observations, and to consider especially the aural record in relation to weather at Champaign.

Acknowledgments

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Methods

For details on the principal method of study we refer the reader to our technique paper (1959). Here we need only summarize. Amplified calls of nocturnal migrants were recorded nightly on tape. The recording was controlled by an automatic timer which sampled 1¹/₂ minutes out of each 10 minutes during the night, providing a 1¹/₂-hour-long tape representing 10 hours. Tapes were audited daily and the time of calling of migrants and the number of each type of call recorded on a data sheet. We noted species names only when we felt certain of the identity of the call. Otherwise the phonetics for the call was recorded and, when possible, a general identification, such as: "warbler, possibly *Oporornis.*"

In computing "flight-call densities" we have, for simplicity, used the area pattern shown in Graber and Cochran (1959:228), though the pattern actually varies somewhat with the sound source.

We have expressed flight-call densities as number of calls per mile, per hour, or per night, following Lowery's (1951) work on flight density. Unless otherwise stated, when we refer to a relative volume of migration (heavy or light), we mean migration volume as indicated by our records of calling of nocturnal migrants. We recognize the difference between high volume of migration and high incidence of calling by nocturnal migrants. Mass flights would go undetected by our system if migrants remained silent.

To obtain data to compare with the audio record, Graber (1) made daily censuses of migrants in local woodlands during at least part of each migration season. (2) checked a local television tower daily and collected specimen data of kills, and (3) made lunar observations of migration on two nights in the spring of 1959.

Our audio station was purposely located in open country and the nearest woodlands were approximately 8 miles away, near Urbana, Illinois. In censusing migrants this same area and the same census route were used daily. The route through open park lands, dense shrub thickets and mature woodland was about 1 mile long and required about one hour (0600–0700) to cover. Only individuals of species known to be nocturnal migrants were counted. Census figures were recorded on field data cards and the day-to-day change in the migrant population was graphed to facilitate comparison with the audio record. The graph was based on a point system in which each apparent departure or arrival of a species in the area, and each obvious change in numbers of individuals of a species, counted a unit on the graph. A new species arrival was counted only when at least two individuals were seen.

We strove for a continuous aural record each season, but equipment failure or power failure caused some gaps in the record. We were still experimenting in the fall of 1957, and the record for that season is particularly sketchy, providing data for only 38 nights in the period from August 17 to October 14. The record for fall, 1958, was uninterrupted and ran from September 7 to October 24. The spring records ran from April 13 to June 1 (1958), and from April 8 to May 30 (1959). Each spring record contained lapses of six nights (not consecutive).

All figures referring to time of day in this paper represent Central Standard Time.

MASS MIGRATIONS-TIMING AND WEATHER AT CHAMPAIGN

Though some migrants were heard on 85–89 per cent of the nights recorded, most of the volume of migration (67–88 per cent) passed on a relatively few nights (23–42 per cent of nights recorded). Figs. 1–2 and Table 1 present data on these mass migrations.

A relationship between mass migration and frontal systems has been recognized at least since the time of Cooke (1888), and a number of authors have reviewed the subject. Most of the mass movements of birds detected in this study were associated with frontal systems—warm fronts in spring and cold fronts in fall.

This association was apparent in the coincidence of timing between the movement of the front and the birds (Figs. 1-2 and Table 2). In fall, 1958,

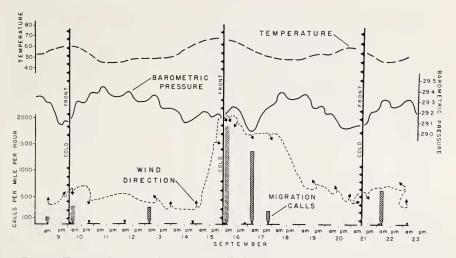


FIG. 1. Timing of nocturnal migration with frontal passage and changes in minimum nightly temperature (in °F.), barometric pressure (in inches) and wind direction at Champaign, Illinois, in September, 1958. Bar graph shows volume of migration as indicated by calling of nocturnal migrants. Black base line indicates night hours, and time markers indicate 12 midnight and 12 noon. Arrival time of first migrants is shown by black apexes.

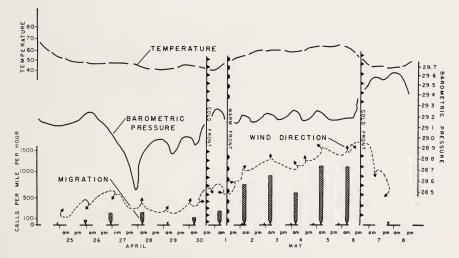


FIG. 2. Timing of nocturnal migration with frontal passage and changes in minimum nightly temperature (in °F.), barometric pressure (in inches), and wind direction at Champaign, Illinois, in spring, 1959. Black base line indicates night hours, and time markers indicate 12 midnight and 12 noon. Arrival time of first migrants is shown by black apexes.

	Tatal	Number	Descent	Total -		Mass	Migration	
Season		of nights with mi-		volume of migration ¹	Number of nights	Per cent of nights ²	Volume	Per cent of total volume
Spring, 1958	3 44	39	89	34,615	9	23	23,270	67
Fall, 1958	47	40	85	59,620	14	35	52,560	88
Spring, 1959	9 46	40	87	90,920	17	42	78,145	86

TABLE	

MASS MIGRATION IN	RELATION TO	SEASONAL VOLUME
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 1 Volume of migration as indicated by calls of migrants per mile per season. 2 Per cent of nights on which any migration was recorded.

heavy migration accompanied each of the six cold fronts which occurred in the study period. When the fronts passed in the night (four times) an increase in calling of migrants began within 20 minutes to two hours after the passage. Two of the cold fronts passed Champaign in the daytime-one at 1200, with the first migrants coming 12 hours later; and one at 1700, with migrants following in five hours.

The greater lag between migrants and fronts which pass in the daytime (versus night) reflects the fact that migration ceases during the day. Frontal speeds varied between 5-25 mph. and averaged about 15. With their own speed plus the speed of the frontal winds, migrants could not consistently remain behind the front without the daytime rest.

In spring, also, migrants lagged behind frontal passage. During the two years studied virtually all of the spring warm fronts passed Champaign in the davtime. Because day length is longer in spring than in fall, one would expect the interval between front and birds to be longer in spring also, and thus our data show it to be (Figs. 1-2).

From the audio data it is possible to obtain some impression of the frequency with which migrants overtake fronts. Assuming a base flight speed of 20 mph for birds, and adding tail-wind data, we calculate that migrants would have overtaken spring warm fronts only once in four mass flights. In this case, May 16-17. 1958, the front's speed was only 5 mph. and the fastest migrants would have overtaken the front about 0300. The migration on this night was very heavy and migrants were possibly "piling up" behind the front.

In fall, migrants overtook fronts in five of six mass flights, but in most cases the closing of birds with fronts would have occurred between 0400 and 0500, i.e., at about the time for the night's migration to end. Consistently the pre-dawn peaks in calling came earlier on mornings when migrants were overtaking the fronts, and the time of the peak in calling appeared to correlate

	1		Wind change	ange		Arrival ¹	Arrival ²		Volume ³
Date	Front	From	From	To	Speed (mph)	time of front	time of migrants	Difference	ot migration
May, 1958									
2-3	Warm	S	NE	s	15	1100-2	0200-3	-15:00	1775
16-17	Warm	S	NE	SE	5	1000 - 16	2300 - 16	-13:00	6400
17-18	Front stationary	onary C. Illinois	C. Illinois (24 hours)	Continues	S-SW	; Migration continues,	ues, but slowing		2625
21 - 22	Warm	S	NW	S	20	1300-21	2100-21	- 8:00	4900
May, 1959									
- 2	Warm	SW	MM	SW	12	1300 - 1	0230-2	-13:30	2700
2-6	Front mov	Front moves to N. Wisconsin (12 hours) Continues S-SE; Heavy migration continues	in (12 hou)	rs) Continu	ues S-SE;	Heavy migratio	n continues		9050/night
15-16	None		NW Calm–SW	m-SW		1300 - 15	0100 - 16	-12:00	930
16-18			Continue	Continues SW-SE		Heavy migra	Heavy migration continues		5885/night
18-19	Warm	S	Continue	Continues S-SE	15-20	0030–19, Hea	0030-19, Heavy migration continues	continues	3935
19-22	Front mov	Front moves to N. Wisconsin (12 hours) Continues S-SE;	in (12 hou	rs) Continu	ues S-SE;	Heavy migration continues	n continues		3780/night
September, 1958	958								
9-10	Cold	NNW	M	N	20 - 25	0240 - 10	0300 - 10	- 0.20	3860
12-13	None		NE	Calm		1600-12	0400 - 13	-12:00	3100
15-16	Cold	NW	$\mathbf{S}\mathbf{W}$	N	5	0130 - 16	0330 - 16	-2:00	12,900
16-18	Front mov	Front moves to S. Illinois ((12 hours)	Continues	N-NW; H	N-NW; Heavy migration continues	continues		6290/night
21 - 22	Cold	NW	SW	NW	17	1200-21	0030 - 22	-12:30	6700
25-26	Cold	NW	SW	NW	16	1700-25	2200-25	-5:00	3100
26-27	Front mov	Front moves to S. Illinois (12 hours)		Continues	NW; Mig	Continues NW; Migration continues, but slowing	but slowing		1660
October, 1958	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~								
4-5	Cold	NW	SW	Z	18	0030 - 5	0230 - 5	-2:00	1600
16-17	Cold	MNW	SW	NW	10	0300 - 17	0200-17	1:00	1700

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with the time of the closing of the gap between birds and fronts, i.e., when the closure occurred later, the peak in calling also occurred later.

Interestingly, on the night of the tower kills in the falls of 1957 and 1958, migrants were pressing the front especially closely, and on the night of the larger kill (1957) birds overtook the front earlier in the night. This is discussed later with the tower-kill data.

In only one instance did a large number of migrants reach Champaign in advance of a front. On October 16–17, 1958, at 0200 the first migrants were heard one hour in advance of an oncoming slowly moving cold front. This shows that migrants will, at times, overtake and pass the front, but in *all* observed cases of mass migration the vast majority of birds trailed the front.

In September, cold fronts which pass through Champaign almost invariably come from the west-northwest, originating on the northwest Pacific coast, and moving eastward to the central Dakotas and Minnesota. In this area (Dakota-Minnesota) the fronts turn decidedly to the southeast and pass ultimately off the Atlantic coast from east-southeastern United States.

In reaching Illinois these fronts sweep an area 2000 miles long and several hundreds of miles wide in northern United States and southern Canada.

Probably, birds from the Pacific northwest which generally represent a different fauna than that found in Illinois do not follow the front across the continent. However, certain species, such as Swainson's Thrush (Hylocichla ustulata), could conceivably come to Illinois from as far as British Columbia behind a front.

In September, the species of migrants which occur in the Champaign area in greatest abundance are probably the Swainson's Thrush, Ovenbird (Seiurus aurocapillus), American Redstart (Setophaga ruticilla), Tennessee Warbler (Vermivora peregrina), Magnolia Warbler (Dendroica magnolia), and Baybreasted Warbler (Dendroica castanea). All of these have large areas of breeding range which lie in the path of the cold fronts. On the other hand, neither the Veery (Hylocichla fuscescens) nor the Hermit Thrush (Hylocichla guttata) is abundant here in migration, yet both species have large portions of their breeding range in the regions covered by the cold fronts. Conversely, the Gray-cheeked Thrush (Hylocichla minima) is a common September migrant here, yet most of this species' breeding range lies north of the frontal sweep. We have no way of knowing how far migrants may follow a front, or, indeed, if they actually follow the frontal path. The aural data suggest this possibility, however.

Despite the similarity which different fronts show in their direction of movement and area of coverage, the volume of migration which follows different fronts is highly variable. In fall the volume of a particular mass movement of birds appears to show a relationship to the time interval between

the end of a mass migration and the subsequent appearance of another cold front. As this interval increases the volume of migration also increases. The relationship was apparent in the fall data both in 1957 and 1958. In the fall of 1958 when the migration-cold front interval was only two days, the subsequent migration lasted only one night, and the volume was 300 calls per hour per mile. For other intervals the figures were: three days-one night of migration at a volume of 400 calls per hour per mile; for three and onehalf days-one night, 600 calls: and for six days-three nights of migration, 1100 calls. This relationship can be explained by the reasonable assumptions that all migrants in an area do not develop the condition of "Zugunruhe" simultaneously, but with the passage of time, more and more birds come into the restless state. When a front passes, those migrants which exhibit nocturnal restlessness take flight. If a second front passes the region soon after the first, relatively few migrants will have attained the physiological state in which they are responsive to frontal passage. If the second front does not pass for several days, more migrants in the region will have become responsive. Thus, successive fronts "sweep" more and more birds southward. In spring this time-volume relationship was not evident.

INITIATION OF FLIGHT

From the time-relationship between arrival of migrants and fronts, it is reasonable to assume that something about the passing of a front initiates the mass flights and that birds do not take wing until the front is past. Devlin (1954:94–95), from observations of the moon and in the field, considered the hour just before nightfall to be the critical time as far as the initiation of nocturnal migration was concerned in spring. He also suggested that migrants do not often take flight in the middle of the night. The fact that there is usually a lag between the time of frontal passage and the passing of the first migrants tends to support Devlin's view. Migrants taking off at night immediately after a front passed would ordinarily overtake it quickly, whereas migrants that start only at sundown or shortly after would be following the front by an interval of the number of hours between the time the front passed and sundown. Ball (1952:67–68) twice observed single birds taking flight in the early morning, but it is not known whether these observations represented mass migration.

Several times calls of nocturnal migrants were heard at Champaign shortly after sundown. The initial calling of migrants was also heard as late as $6\frac{1}{2}$ hours after sundown following the passage of a front. Presumably, no matter what time of the day a front passes, nocturnal migrants will respond at sundown if the proper conditions (established by the front) still obtain.

Of the factors which the front may change, wind, temperature, and pres-

sure have been most commonly considered as being important to migration. Devlin (1954:95) believed that certain conditions of wind and temperature at sundown stimulated migration. Lowery (1951) showed that migrants generally moved with the wind, and indirect evidence presented by Bennett (1952) and several other authors supports his data. Bagg *et al.* (1950) presented an excellent discussion of migration in relation to barometric pressure and other meteorological phenomena.

It is worth while to consider the audio record in relation to such factors.

Migration and Surface Winds.—In fall, 1958, virtually all (93 per cent) of the calling of nocturnal migrants occurred during hours when surface winds were from the north-northwest (76 per cent) or calm (17 per cent), notwithstanding the fact that winds were predominantly southerly during the migration season (Figs. 3–5). Twenty-seven per cent of the night hours were calm.

In spring, 1958, most of the calling (72 per cent) occurred during hours when surface winds were south-southwest (54 per cent) or calm (18 per cent), though the winds were predominantly northerly. Twenty-three per cent of the night hours were calm. In spring, 1959, most of the calling (84 per

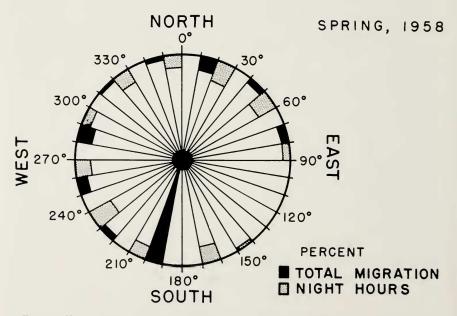
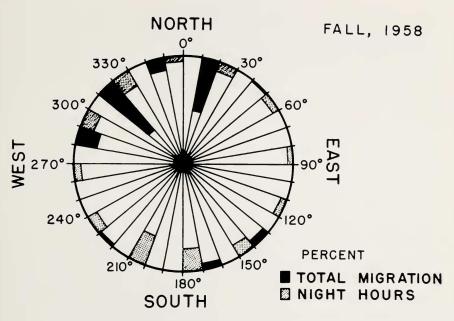


FIG. 3. Total seasonal volume of migration occurring with specific wind headings. Gray shading shows per cent of night hours during the season that wind held a specific heading. Black shading shows per cent of total migration occurring *with* the wind heading indicated.



NORTH SPRING, 1959 0° 330° 30° 300° 60° 90°EAS S 270° 120° 240 PERCENT 150° 210° TOTAL MIGRATION 180° NIGHT HOURS SOUTH

FIGS. 4 (above) and 5 (below). Total seasonal volume of migration occurring with specific wind headings. For key, see Fig. 3.

cent) occurred when winds were from the south-southeast (58 per cent) or calm (26 per cent). Sixteen per cent of the night hours were calm. Maximum surface winds coinciding with heavy migration did not exceed 12–14 mph.

We have not made similiar calculations for winds aloft because of a lack of detailed data, but on an average, winds above 1500 feet show a clockwise rotation of 30° and an increase in velocity of about half the speed of surface winds.

Assuming northward flight in spring and southward flight in fall, it is clear that birds migrated with the winds. The question remains as to whether frontal passage was associated with a change in wind which favored migration. Figs. 1–3 show definitely in the affirmative. In fall, migration occurred when the wind shifted from southwest to northwest, and such a shift usually coincided with the passage of a front from the northwest.

In spring, migration occurred with a wind-shift from the north to the south. Often a 360° rotation in wind direction from southwest to northwest to north (coinciding with a cold front) to northeast to southeast (coinciding with a warm front) to south-southwest preceded by 48 hours the very heavy spring migrations. Such wind-shifts were usually associated with the passage of fronts, but one of the heaviest migrations in spring (May 17–18), 1959, did not coincide with a definite frontal system though a wind-shift west to south did occur. On this occasion southerly winds continued for at least six nights and so did the migration. The passage of a warm front on May 19 did not cause an increase in the volume of migration. The conditions which favored migration were already established before the front arrived. This observation indicates that a definite frontal system, per se, is not important to migration, though the conditions which favor migration are usually associated with the passage of a front.

The change in wind which precedes the arrival of migrants occurs relatively quickly, often in a matter of one or two hours. Velocity as well as direction is usually involved, and the change is one which an animal might detect very easily.

On only four nights, May 25–26, 1958, April 26–27 and May 22–24, 1959, was there notable migration apparently against the wind. Winds aloft (second standard level) were favorable (southerly) for the April date, but not for the migrations on May 22–24. The lateness of the dates suggests the possibility that migrants are more likely to move under unfavorable circumstances late in the season. This same view was expressed by Cooke (1888: 16–25), who believed that late in the season (spring) some migration occurred on every night.

Migration and Changes in Temperature, Humidity, and Pressure.—Changes in temperature, pressure, and humidity which accompany passage of a front

might also conceivably be detected by migrants.

In fall, most waves of migration coincided with periods of relatively high night temperatures, though with the 24-hour trend toward falling temperatures (Fig. 1). In spring, mass migrations came consistently in periods when temperatures were rising, often following a short period when night temperatures were lower than average (Fig. 2). The tendency for birds to migrate on warm nights was more pronounced in spring than in fall.

Daily fluctuation in temperature was so great in both spring and fall that it seemed unlikely that migration could be triggered by the subtle temperature changes which accompany a front, especially in view of the fact that at sundown, the presumed time of take-off, the temperature is usually falling steeply. Temperature and humidity are so closely interrelated that it is difficult to evaluate them separately. Humidity as indicated by dew-point temperature tends to follow the curve of minimum nightly temperatures. Dew-point is less variable than temperature, and changes in dew-point are usually subtle.

In fall, at least, no particular condition of temperature or humidity correlated with migration if the winds were adverse (note conditions during the period September 15–18, 1958, in Fig. 1). In spring, warming temperatures and increasing humidity so consistently accompany southerly winds that the factors, again, are difficult to evaluate separately.

At Champaign, the beginning of heavy migration usually accompanied rising barometric pressure in fall and falling pressure in spring (Figs. 1-2). Though it does not fluctuate so much as temperature, pressure is highly variable. However, the pressure changes which accompany a front are not usually extraordinary, so pressure change (at least by itself) seems unlikely as a factor to initiate migration.

In summary, the factors which most consistently precede or accompany the initial wave of birds in a mass migration are: in fall, wind direction change from southwest to northwest, relatively high night temperature but with falling trend, and rising barometric pressure; in spring, wind change from southwest to north to southeast to south, rising temperature, and falling barometric pressure.

Of these factors, the wind changes correlate most directly with fluctuations in volume of migration. The audio data indicate that it is the wind which probably exerts the dominant influence in initiating and halting a mass flight.

Once migration was initiated, it continued past a point of observation until the migrant swarm passed, if the proper conditions held. In fall, mass migration appeared to discontinue if surface winds became southerly. Cessation of fall migration, or at least of nocturnal calling, coincided also with relatively low night temperature and high barometric pressure, though not invariably.

In spring, migration was discontinued when winds switched from south-

Tenths of cloud cover	Per cent of time with condition	Per cent of migration occurring
Fall, 1958		
0-5	67	44
6-9	13	9
10	20	47
Spring, 1958		
0-5	55	36
6-9	25	45
10	20	19
Spring, 1959		
0-5	30	39
6-9	20	27
10	50	34

TABLE 3

ANALYSIS	OF]	MIGRATION	AND	CLOUD	COVER
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erly to northerly. Again not invariably, such a change was accompanied by low night temperature and high pressure. Thus on May 2-6, 1959, heavy migration continued nightly with southerly winds until halted by a windshift (with a cold front) from the south to the north-northwest. This is an example of the situation described by Bagg et al. (1950:18) that in spring "pronounced movement will take place . . . through a given region during the interval between the passage of a warm front . . . and the subsequent arrival of a cold front."

Cloud Cover and Migration .- In view of the interesting work of Sauer (1958) and Bellrose (1958) on celestial orientation in birds, it is worth while to consider the audio record of migration in relation to cloud cover because opaque overcast could conceivably interfere with celestial orientation.

Tables 3 and 4 present data on migration and cloud cover. Table 3 indicates that migration is not particularly reduced on nights with opaque overcast. No consistent tendency is shown and the condition of overcast appears to be incidental to other factors as far as volume of migration is concerned.

Table 4 summarizes data on migration and opaque overcast in greater detail. On the nights of May 2-3 and September 15-17, 1958, and April 26-27 and May 17-18. 22-23, 1959, heavy migration coincided with complete overcast. Birds flying at elevations of a few hundred feet could not have seen the stars on those nights. In one case (September 15-17) opaque overcast lasted as long as 59 hours in the Champaign region, and in all of the cases mentioned the overcast was widespread, extending over several states. It is possible that in most cases birds could have been flying above

		Peri	Period of							
		nbodo		Lowe 10ths	Lowest layer	Secor 10ths	Second layer	Third layer	d layer	Concernation
Hours	Volume	Start	End	1	(feet)		(feet)		(feet)	of overcast
00				ц ч	800 700	99	1300	9	2300	III., S. Wise., Ind.,
- 00	1775	21900	3-1900	000	200 200	+ 1 4	1900			Mo., Iowa, Minn.
$1958 \\ 2000 - 2300$	00001	0000 11	0000 21	10 5	3800 u	⊐ °?	1600	л 67	2300	III., S. Wise., Mich., Ind., E. Mo., E. Iowa
00	12890	0060-e1	1/-2000	28	$1200 \\ 400$	∽ ¢1	$4000 \\ 800$	nn		
	10265			10 8	$3500 \\ 400$	10 u	8000	n		Ill., Wisc., Mich., Ind., Ky., Tenn., Miss., N.
88				10	300	n		n		La., Ark., Mo., Iowa, Minn.
2000 - 2300	1698	26-1100	27-0900	4	1300	9	2300	n		Ill., Wisc., Mich., Ohio, Ind., Ky.,
88				10	10000	n		n		Tenn., N. Ark., Mo., Iowa, Minn.
-00	7834	17-1100	18-0600	10	1200 - 1600	n		n		Ill., S. Ind., Ky., Tenn., Mo., SE Iowa
				202		∞∞	$2000 \\ 2000$	п		
2000- 2300 0000-	2112	22-0800	23 - 2200	0100	600 400 200	n		n n		Ohio, N. Ind., W. Ky W. T. Ind., W. Ky
8				10	300	n		п		E. Tex., Okla., Kans.,

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at least the lower cloud layers, but in all of the cases cited, migrants probably began their night's migration in Illinois under opaque overcast without having seen direct sun or other starlight for as many as 14 hours.

The importance of favorable wind conditions to migration has already been stressed. With only one exception (April 26–27, 1959) heavy migrations under overcast occurred with favorable winds. This fact implies that migrants were able to identify wind direction without the stars for orientation.

It is also conceivable that migrants fly at such times even though they are dis-oriented, but this seems unlikely in view of the frequency with which migration and overcast coincide.

COMPARISON OF TOWER KILLS AND AUDIO RECORD

Brewer and Ellis (1958) presented data on kills which occurred at the WCIA tower, Champaign County, Illinois, between 1955 and 1957. Our sound station was located approximately 8.5 miles southeast of this tower, and since fall, 1957, we checked the tower daily in migration season. The major kills occurred in fall on the nights of September 21–22, 1957, and September 15–17, 1958. There were other kills, but none in which more than six specimens were found.

Comparison of our recordings with kill data (Table 5) shows some interesting similarities and differences.

The number of types of calls correlated well with the number of species killed, but in each case more species were heard calling than were killed. The record for individual species suggests a possible differential rate of calling for different species from night to night, and points out one of the pitfalls for the investigator who depends entirely on the audio technique.

However, there appears to be a rough correlation between numbers of thrushes calling and thrushes killed. This ratio for all thrushes for the three kills was 8:4, 90:60, and 70:64 per cent. In each case per cent of total calls exceeds per cent of total kill, which indicates that the thrushes are vociferous by comparison with other species, for instance, the Bobolink (*Dolichonyx oryzivorus*).

Correlation between flight-call density and flight density as determined from tower-kill data was variable. The smallest kill occurred on the night (September 15–16) when the *highest* call density was recorded. The density ratio (call:kill) for this night was 1:1.7. For the other two nights the ratios were 1:3100 for both. The density as determined from kill data is consistently higher. Cochran and Graber (1958) showed that migrants are apparently attracted to tower lights, a fact which could tend to raise densities calculated from kill data out of proportion to the true density.

All three kills were associated with mass migration accompanying cold fronts from the northwest and 10/10 opaque stratus or strato-cumulus cloud

	Comparison of Audio Record and Tower Kill	ECORD AND TOWER KILL	
Audio record species	Per cent of all calls	Tower kill species	Per cent of birds killed
	September 21 -22, 1957	21-22, 1957	
Hylocichla A	ŝ	Swainson's Thrush	2
Hylocichla B	5	Gray-cheeked Thrush	2
Hylocichla C	0.6		
Bobolink	1	Bobolink	0
Total	9.6	Total	4
Number of types of calls	44 plus	Number of species killed	25
Flight-call density	7235 calls/mile/night	Flight density	226,171 birds/mile/night
	September 15–16, 1958	5-16, 1958	
Hylocichla A	74	Swainson's Thrush	10
Hylocichla B	10	Gray-cheeked Thrush	50
Hylocichla C	6		
Total	90	Total	60
A more of types of calls	6	Number of species killed	4
№ ight-call density	12,900 calls/mile/night	Flight density	21,747 birds/mile/night
	September 16-17, 1958	(6-17, 1958	
IIy'ocichla A	51	Swainson's Thrush	39
Hylocichla B	2	Gray-cheeked Thrush	22
Hylocichla C	12	Veery	33
Bobolink	1	Bobolink	11
Total	71	Total	75
Number of types of calls	20	Number of species killed	17
Flight-call density	10,265 calls/mile/night	Flight density	319,684 birds/mile/night

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cover. At Champaign on the night of September 21–22, 1957, the lowest cloud layer did not fall below 3500 feet. On both September 15–16 and 16–17, 1958, the lowest layer was 3500–3800 feet early in the evening but fell to 300–400 feet by 0600.

Heavy fall migrations also occurred on September 7-8, 12-13 (highest density of season), and 14-15, 1957, and on September 7-8, and 21-22, 1958. These instances were not accompanied by continuous opaque cloud cover, and produced no kills.

There were no large kills at the tower in spring, notwithstanding the fact that on the night of May 17–18, 1959, there was opaque overcast with clouds as low as 600 feet, and the call density was 7834 per mile, i.e., higher than the density (7235) recorded on the night of the kill in September, 1957. This was the only incidence in which the volume of migration exceeded 7000 calls/mile and coincided with relatively low opaque overcast without producing a kill.

It is obvious that overcast may be only a contributing factor to the kills. It was suggested above that the occurrence of kills at the WCIA tower might be related to the circumstance of migrants overtaking a front. Kills did occur on nights when migrants caught up with slow-moving fronts, and the largest kill occurred when birds overtook the front earlier in the night.

On October 16–17, 1958, migrants passed a front at Champaign, but under clear skies. and no kill occurred. Again on May 16–17, 1958, migrants overtook a front at Champaign, but there was not complete overcast and no kill. On May 17–18, 1959, when heavy migration coincided with opaque overcast no kill occurred, but neither was there a frontal system involved.

Newman (1958:4) described a number of kills which occurred in fall, 1957, well behind a front, but our audio data suggest that at Champaign it was the combination of circumstances—heavy migration, complete overcast, and slow-moving front (which migrants overtake)—that effected large kills. Under clear skies migrants will overtake a front and continue to fly even into adverse winds without becoming confused. This may imply that night migrants are utilizing celestial orientation. On the other hand, as long as migrants are flying with favorable winds behind a front, no kill will occur even if skies are completely overcast.

COMPARISON OF AUDIO RECORD WITH FIELD OBSERVATIONS

A number of valuable studies of migration have been conducted by the indirect method of observing changes in the local population of migrants during the daylight hours (Bennett, 1952; Raynor, 1956). Though our general conclusions are similar to Bennett's (1952) for Illinois, our data suggest that the indirect method at times may be misleading.

Correlation between peaks of migration as determined by nocturnal audit-

ing and by diurnal field observations was poor (Fig. 6). Indications by audio record of heavy migration were not always corroborated by the diurnal observations (note records for September 13, 1957, May 4–6 and 18, 1959). Conversely, indications of migration by diurnal observation were not always evident on the taped record (note records for September 26–28, 1957, and May 10, 1959). The very heavy migration (audio record) of September 12– 13, 1957, continued at least until daylight, yet a thorough search on September 13 of several woodlands within a radius of 10 miles of the audio station revealed very few migrants. Arvin (in Nolan, 1958:41) reported a similar occcurrence in southern Texas. He heard calls of migrants on 13 consecutive nights in August but never found large numbers of migrants during the day in this period. Nolan (1958:34) stated that the cold front of September 21–22, 1957, did not precipitate notable migration in the Illinois region, though the audio record for that period shows heavy migration.

There are several possible explanations for these discrepancies. When migration calls are detected at night but no migrants are observed in the daytime, it is conceivable that the migrant swarm might completely pass an area during the night, or that the record of nocturnal calling gives us an exaggerated impression of large-scale migration, for calls of birds in the night may be more conspicuous than grounded migrants. Note in Fig. 6 that the record of diurnal observation tends to be less fluctuating than the record of calling. It is also conceivable that the local population of migrants could turn over completely, yet appear unchanged to the observer, i.e., if the observer counted 20 Swainson's Thrushes and 10 Magnolia Warblers on two consecutive mornings he might logically assume that the migrant population had not changed, even though the individual birds were entirely different on the two mornings.

The situation in which a change in the migrant population is evident, though no migration calls have been detected, may reflect the inadequacy of the audio technique. The difference between the audio and field records in late September and October, 1958 (Fig. 6), is of special interest here. The audio record in this period was largely negative, while the field record showed migration. It has already been shown (Figs. 1, 2) that heavy migration as indicated by calling tends to occur on relatively warm nights. If temperature does affect the rate of calling, reduced calling on the cooler nights of late September and October could account for the difference in volume of migration as indicated by field observation and flight-call counting. Any other factor that affects the rate of calling of migrants would, of course, affect the correlation (or lack of it) between the two sets of data.

Some Species Records.—One of the most promising aspects of study with the audio technique is the acquisition of detailed information on migration patterns and habits of individual species. Such information depends upon the investigator's ability to precisely identify nocturnal notes. The matter of identification of the night call notes is complicated because certain species have what amounts to a night vocabulary, using a particular call only during nocturnal migration, or in daylight only at the beginning or termination of a flight. Ball (1952:49) has discussed such call notes of the *Hylocichla* thrushes.

Some species, however, utter night calls which are the same as or similar to those used in the daytime. The Dickcissel's (*Spiza americana*) night call is one which can be heard on the nesting territories frequently in daytime, especially in late summer, though it is seldom used after spring migration and before juveniles begin to appear in the nesting areas. Cuckoos utter full "songs" in flight regularly in spring, though they also use double- or triplenoted flight calls.

The real problem groups as far as identification is concerned are the calls of a number of species of warblers and small sparrows. Their "chips" or "lisps" are sharp, short, high-pitched calls which do not differ distinctively from species to species. Many of these identifications can probably be worked out with careful field study and careful study of recorded calls. Until this is done the investigator cannot realize maximum benefit from the audio method.

Whole groups of birds may migrate in silence. For instance, we have very few records of duck calls (in contrast to geese), and it seems probable that ducks are generally silent in night migration. It is also possible, of course, that very few ducks have crossed our station.

Fig. 7 shows the records of calling for several species of nocturnal migrants in the spring, 1958 and 1959, and provides information on annual variation in migration patterns. Except in the case of the Yellow-shafted Flicker (*Colaptes auratus*), migration came earlier in 1959 than in 1958. Bagg (1958) discussed the spring migration of 1958 in North America in relation to weather and pointed out that migration lagged before mid-April. Nolan (1958:356), in summarizing field notes for the Middle-Western prairie region, stated that the migration was late until mid-April, and that though the schedule caught up in late April and May, migration waves did not attain remarkable proportions. In contrast, the spring migration of 1959 in the prairie region was ahead of schedule (Newman and Lowery, 1959). These statements are corroborated by the audio record (Fig. 7).

Lunar observations.—We made lunar observations at our sound stations for only two hours, one each on April 24 and May 19, 1959, both times between 2300 and 2400, the hour when highest densities are usually recorded in lunar observations.

On April 24 the hour-station-density for 2330 was 1558 birds. No migration was recorded by the sound station in this hour and the flight-call density for the entire night was 270 calls.



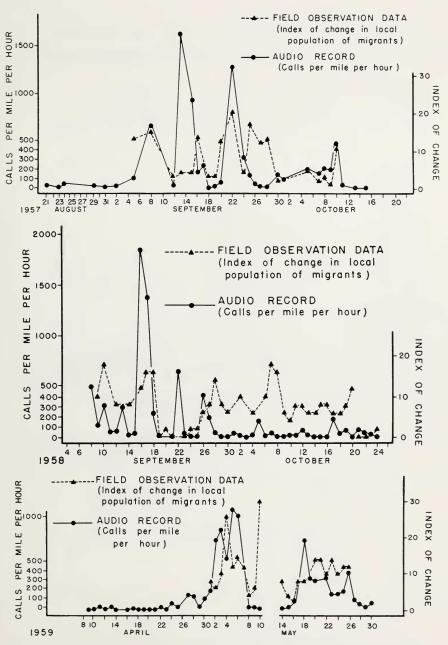


FIG. 6. Records of calling of nocturnal migrants compared with daily field observations on local population of migrants. Index of change indicates observable day-to-day change in migrant population. Not all points are plotted, but all fall on the graph lines.

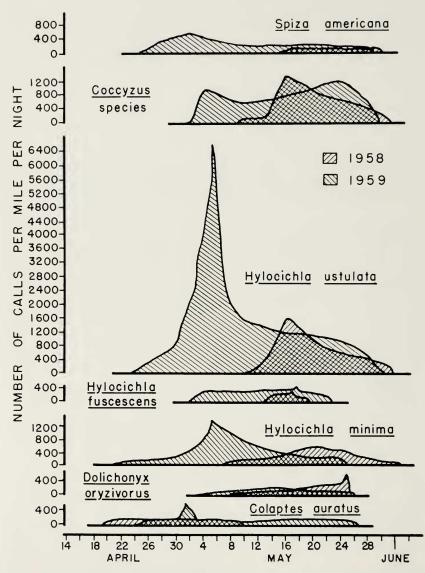


FIG. 7. Records of nocturnal calling for 7 species of migrants at Champaign, Illinois, in spring seasons of 1958 and 1959. Migration did not occur on every night, and figures show only an outline of peaks in migration.

On May 19 the hour-station-density (from lunar observations) for 2330 was 2224 birds. The hour-flight-call-density was 231 calls and the density for the night, 3666.

Both methods, then, show the same general difference, i.e., heavier migration on May 19. The magnitude of the difference indicated by the two methods (1:1.4 for lunar data and 1:13.6 for audio) indicates the expected greater variability inherent in the latter method.

LITERATURE CITED

BAGG, A. M., W. W. H. GUNN, D. S. MILLER, J. T. NICHOLS, W. SMITH, AND F. P. WOLFARTH 1950 Barometric pressure patterns and spring bird migration. Wilson Bull., 62:5–19.

BAGG, A. M.

1958 The changing seasons. Aud. Field Notes, 12:320–333.

BALL, S. C.

1952 Fall bird migration on the Gaspé Peninsula. Peabody Mus. Nat. Hist. Yale Univ. Bull., 7:1-211.

Bellrose, F. C.

1958 Celestial orientation by wild Mallards. *Bird-banding*, 29:75–90.

BENNETT, H. R.

1952 Fall migration of birds at Chicago. Wilson Bull., 64:197-220.

BREWER, R., AND J. A. ELLIS

1958 An analysis of migrating birds killed at a television tower in east central Illinois, September 1955–May 1957. Auk, 75:400–414.

- COCHRAN, W. W., AND R. R. GRABER
- 1958 Attraction of nocturnal migrants by lights on a television tower. *Wilson* Bull., 70:378–380.

COOKE, W. W.

1888 Report on bird migration in the Mississippi Valley in the years 1884 and 1885. U.S. Dept. of Agric., Div. Ec. Orn. Bull., No. 2. 313 pp.

DEVLIN, J. M.

1954 Effects of weather on nocturnal migration as seen from one observation point at Philadelphia. *Wilson Bull.*, 66:93–111.

GRABER, R. R., AND W. W. COCHRAN

1959 An audio technique for the study of nocturnal migration of birds. Wilson Bull., 71:220-236.

LOWERY, G. H., JR.

1951 A quantitative study of the nocturnal migration of birds. Univ. Kans. Publ. Mus. Nat. Hist., 3:361-472.

NEWMAN, R. J.

1958 The changing seasons. Aud. Field Notes, 12:4-9.

NEWMAN, R. J., AND G. H. LOWERY, JR.

1959 The changing seasons. Aud. Field Notes, 13:346–352 + cover plates.

NOLAN, V., JR.

1958 Regional reports. Spring migration. Middlewestern prairie region. Aud. Field Notes, 12:356–358.

RAYNOR, G. S.

SAUER, E. G. F.

1958 Celestial navigation by birds. Sci. Amer., 199:42-47.

ILLINOIS NATURAL HISTORY SURVEY, URBANA, ILLINOIS, NOVEMBER 23, 1959

¹⁹⁵⁶ Meteorological variables and the northward movement of nocturnal land migrants. Auk, 53:153–175.